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Speciation in the Neotropics and the Founder Principle

Francisca C. do Val[1]

ABSTRACT: The association of bottleneck effects and speciation patterns observed in South American flies *Drosophila paulistorum*, lizards *Anolis chrysolepis* and *Mabuya arajara*, and frogs in the genus *Cycloramphus* is briefly examined. Bottleneck effects as consequences of reduction of population sizes in situ seem to be a relevant factor to speciation, distinct from isolation through large-scale fragmentation, environmental differences, or genetic drift.

IN THIS PAPER I REVIEW BRIEFLY some relatively well studied cases of speciation in South America, examine the current connotations of the founder principle as related to these examples, and discuss whether founder or bottleneck effects can be invoked as having played significant roles in these speciation events. I introduce no new information, but only reanalyze a small number of cases, some of which have been presented in the literature as examples.

FOUNDER PRINCIPLE: ISLANDS VERSUS CONTINENTAL AREAS

In a review of the founding of populations, Carson and Templeton (1984) distinguished founder-induced speciation from founding events whose primary role would be only to establish geographically isolated populations. Earlier, Templeton (1980) regretted the lack of distinction between "the several types of founder principles in speciation." According to him, such a distinction should be essential for incorporating population genetics into both modeling and empirically analyzing the role of the founder effect in speciation.

Carson (1982), discussing the "organization theory of speciation," separated "disorganization by founder events" from "disorganization in situ by reduction of population size to a vestige." It seems to me that in both situations, special effects peculiar to each of these phenomena may be relevant to speciation events. The distinction between founder (one type of bottleneck) and bottleneck effects fits Carson's classification.

Carson and Templeton (1984) restricted themselves to the Hawaiian fauna and flora for examples of "virtually unequivocal dispersal by founder individuals," and concluded, after specifying and carefully discussing a number of assumptions, that the occurrence of founder-induced speciation is a very rare event. In the same review, they expressed their feeling that data on continental and peripheral subspecies do not provide compelling examples of incipient species, contrary to Carson's earlier view (1959); the continental areas referred to are New Guinea and North America. The authors based their opinion on two factors: first, the isolation would not be very marked, and second, the colonizing population would not be small enough to permit sufficient genetic reorganization.

Peripheral isolates of North American organisms (among them, many species of *Drosophila*) are likely to undergo a more or less continuous ebb and flow of population pressure, but are vulnerable to periodic recolonization and genetic swamping from the main body of the species. Such situations would produce ("mimic") conditions very similar to, but distinct from, features of the founder effect (Carson and Templeton 1984).

The "central-marginal model" (reviewed by Brussard 1984) as proposed for the North American geographical situation, although in part corroborated by studies of neotropical

[1] Universidade de São Paulo, Museu de Zoologia, C.P. 7172, 01051 São Paulo, Brazil.

species (e.g., *Drosophila willistoni*), does not apply to other speciation patterns observed in neotropical organisms.

Although it is theoretically valid to think of a single gravid female flying, or being blown, from one point to another and founding a new population by dispersion (colonization) in the Hawaiian archipelago, it is possible to suppose that in some cases, speciation could have occurred when more than a single female (i.e., a small group) was isolated from a larger ancestral population by ecological barriers arisen after dispersal. Another possibility is that a small group may have spread to the next island and then gone through a bottleneck resulting in Carson's (1982) "disorganization in situ by reduction of population size to a vestige." The congruence of patterns observed within the Drosophilidae, for instance, seems to indicate that vicariant forms are not impossible in Hawaii.

How small a sample is required for founder events to have a major role in speciation? Wright (1977: Chap. 13), in his shifting balance theory, has shown that the population will wander off its adaptive peak when a "minimum size" is reached (discussion in Carson 1982).

Progress has been achieved mostly in the understanding of details associated with the founder principle and the genetics of speciation. It is my impression, though, that the concept should include continental organisms and vicariant patterns, for it might be erroneously considered to be strictly associated with colonization and differentiation via dispersal, especially in extreme situations such as distant oceanic islands.

SOME NEOTROPICAL FEATURES

In the discussion that follows I refer to some South American morphoclimatic domains (Ab'Saber 1977*a*), namely, the large "core areas" of the Hylaea (the Amazonian rain forest), the Atlantic forest, and the northeastern *caatingas*. Except for the Atlantic forest, which occupies a latitudinally long and narrow belt, the other domains are broadly polygonal, and wide and complex transitional areas exist between them (discussion in Vanzolini 1972).

For the present purpose, it is also important to mention Quaternary paleoclimatic cycles. The drastic and rapid (hundreds to a few thousand years) climatic changes during the Pleistocene and Holocene in South America have been studied by several authors (Ab'Saber 1977*b*, 1982, Damuth and Fairbridge 1970, Fairbridge 1976, Suguio et al. 1979). The alternation of dry and wet episodes in relatively short geological time resulted in a mosaic of soils, floras, and faunas. Large continuous areas of rain forest existing during the wet periods were fragmented into a number of patches, separated by open formations during the succeeding dry episodes. The isolates have been called "refuges" by analogy to the ice-free areas of Holarctica during glaciations (review in Vanzolini 1981).

It has been stressed that a search for speciation mechanisms peculiar to neotropical taxa is no longer necessary. The biogeographical information from the analysis of northern South American organisms added to the understanding of Pleistocene climatic changes made evident that an orthodox geographic speciation model is prevalent (Simpson 1977).

SPECIATION IN NORTHERN SOUTH AMERICAN GROUPS

Simpson (1977) briefly reviewed the best-studied cases of differentiation and speciation in South American refuges: Haffer (1969) on birds, Vanzolini and Williams (1970) on the lizard *Anolis chrysolepis* species group, Spassky et al. (1971) on *Drosophila paulistorum*, and several authors on heliconiid butterflies. In these cases and in the examples in the following sections, there is evidence from biogeographical data, corroborated by knowledge of Pleistocene climatic changes, that during certain critical dry periods the forest-associated fauna was restricted to patches of favorable environments. Many of these postulated refuges were "small," i.e., a few percent or less of the

original area, and isolated populations of a given species could have ranged from one or a very few individuals to a moderately small sample. Therefore, in most cases, a bottleneck or drastic reduction of population size event probably occurred, and it is difficult to imagine that differentiation from the ancestral population did not occur due also to sampling (bottleneck) effects.

Among the neotropical organisms considered here, the *Drosophila willistoni* species group, including the incipient species of *D. paulistorum*, can be best compared to the Hawaiian *Drosophila* in an investigation of the role of bottleneck effects in the genetics of speciation. This species group has been studied intensively by geneticists during the past 40 years (review by Dobzhansky and Powell 1975, Ehrman and Powell 1982). Although information on many aspects of the natural history, ecology, and geographic distribution of its members is still very incomplete, much is known about their genetic structure.

Ehrman and Powell (1982) mentioned that "the different degrees of divergence among taxa of the *willistoni* group can be related to a sequence of events classically thought to represent various stages in the speciation process."

The chromosomal polymorphism patterns of the incipient species of *Drosophila paulistorum*, as pointed out by Kastritsis (1967), do not follow the model where chromosomal variability tends to be greater at the center than at the margins of the distribution. Obviously, the neotropical areas where these incipient species occur are very different from those where Nearctic species of the genus *Drosophila* have been studied. The northern South American isolates of forest are orogenically determined. These peripheral highlands functioning as refuges kept alive samples of the once widespread ancestral population. The peripheral isolates, upon expansion, would meet in central Amazonia. According to Vanzolini and Williams (1970), in the central area, "the patterns are complex and confuse"; there, recombination, hybridization, or fusion of the former isolated gene pools may happen when the forest returns.

According to Kastritsis (1967), there is no evidence that the incipient species of *paulistorum* "have passed through the completely or nearly homozygous chromosomal state before becoming isolated." *Drosophila pavlovskiana*, which arose from the same ancestral population, could be an exception. The *paulistorum* semispecies share a rather large number of chromosomal polymorphisms while also being polymorphic for new combinations. Among the alternative historical explanations for the observed pattern, Kastritsis (1967) mentioned that "large sections of the original population may have been cut off, gradually became reproductively isolated, and later became sympatric again." He also examined the possibility that marginal populations may undergo speciation while retaining some of the original polymorphisms, and then replacing them with new combinations as speciation progresses. The refuge concept for the neotropical region was suggested after Kastritsis' work. Probably, generally unfavorable conditions caused "small sections" of the original population rather than "large sections" to be cut off.

Winge (1971) studied chromosomal polymorphisms in *Drosophila willistoni*, and observed that racial diversification seemed to be accompanied only by differential distribution of chromosomal inversions.

The semispecies of *Drosophila paulistorum* show pronounced sexual isolation among themselves. Ehrman (1960, 1961, 1965; review by Ehrman and Powell 1982) had evidence showing that sexual isolation apparently was controlled by polygenes scattered in every one of the three pairs of chromosomes (two autosomes and one sexual). "The many genes controlling the sexual preferences produce additive effects, the sum of which makes the bar to crossing nearly complete between the semispecies" (Ehrman and Powell 1982). These authors concluded that the different populations that gave rise to the semispecies have diverged genetically, developing different coadapted gene complexes.

As in the Hawaiian Drosophilidae, it seems that one of the principal systems affected by the isolation in refuges and reduction of population effective size is the very complex

coadaptation system involved in mate recognition and sexual behavior.

Carson (1982) pointed out that "premating isolation between individuals drawn from separate populations appears most often to be an incidental adjunct of the differential adjustment of the genomes within the two separate populations." It "seems to be a principally secondary effect emerging from fine-tuning of the sexual reproduction system." Also, "the fixation of chromosomal changes is likely to be merely an incidental accompaniment of small population effects and forced selection for reorganization as the species is formed."

Summarizing, the speciation patterns observed in the *paulistorum* semispecies may be attributed to the reduction in situ of population size (bottleneck events), the favorable genotypic endowment of the individuals that originated the semispecies, the maintenance of heterozygozity and inversion arrangements, and the appearance of new inversions and shifts in the sexual recognition system. In spite of all the information available, it is not clear whether there is a "crucial" pivotal genetic step or whether speciation can take place only when a number of factors are added.

The *paulistorum* incipient species, and the species of the *willistoni* species group in general, do not show phenotypic differentiation as found in the Hawaiian relatives. On the other hand, among lizards, birds, and butterflies, a great many external morphological differences seem to be associated with the isolation periods and bottleneck effects in the forest refuges of northern South America. The analysis and interpretation of patterns found in the lizard *Anolis chrisolepis*, for instance, were based on morphological stability or variability of characters within geographic areas. In this case, sexual dimorphism is observed in many meristic traits, body proportions, and dewlap patterns.

A STUDY OF THE BRAZILIAN NORTHEAST

Vanzolini (1981) discussed the differentiation of reptiles in small and large enclaves of forest in the Brazilian *caatingas*. The *caatingas* constitute a large Brazilian morphoclimatic domain, with approx. 800,000 km^2, covered by characteristic xerophytic vegetation. The climate is semiarid and very irregular. Evaporation exceeds precipitation during a significant part of the year. There are frequent disastrous drought years. Many enclaves of forest, locally called *brejos*, varying at present in area from a few hectares to tens of square kilometers, are found in the core area of the *caatingas*. Most of these are determined by topographical features, and may occur at the foot, on the slopes, or on the tops of mountains or ridges. A concentration of permanent springs related to geological structures make possible the existence of forest in some *brejos*, despite the low and irregular rainfall.

Vanzolini's main interest in these enclaves was to gather evidence for a possible recent connection between the Hylaea and the Atlantic forest. He supposed that if these separate forest domains had been connected recently, the mesic enclaves of the northeast would be relics of this connection and the study of their fauna should "bear witness to the fact."

Vanzolini (1981) studied the lizard fauna of small enclaves and observed that the first expected characteristic is the reduced number of forest species found: "No more than three or four being obvious at any place, against 12 to 15 in the main body of the Atlantic forest and 20-odd in the eastern Hylaea." He pointed out that this impoverishment is selective and that each small enclave has its own set of forms. Another important characteristic observed is that called by Williams (1977) the "Belém Park effect." Vanzolini (1981) reported that in different small relictual woods, certain rare species of lizards are found in abnormal abundances, more than 20 times those found in Amazonia. "These abnormal densities may very possibly bring the involved species into competition, which is rather unlikely in the sparsely inhabited main forests." The Belém Park effect could be something similar to the "flush" of a local population after a phase of drastic reduction (bottleneck). Another

important aspect is that "the fauna of the surrounding open formations penetrate the small enclaves of forest at least to forage, if not to breed" (Vanzolini 1981).

Quoting again from Vanzolini (1981): "These features of the lizard fauna of small enclaves clearly indicate that a small refuge is not a random sample of the primitive forest, but has a personality of its own. The forest species surviving in it live in an entirely different context than the original habitat. Their survival means adaptation, i.e., change under very strong selective pressures. Rapid differentiation is to be expected. A very interesting, if incidental, consequence of the interaction of the fauna of refuges with that of the surrounding open formations is that it precludes the direct application to small enclaves of the concept of 'insular biogeography,' which makes no provision for fishes foraging on trees."

A most interesting case detected by Vanzolini during the study of a relatively large enclave called the *Cariris* was the differentiation of the lizard *Mabuya arajara*. The enclave studied is not an intact large forest patch, but like all others left in the northeast, has been decimated by agriculture. Nevertheless, typical forest-associated species were found surviving there. *Mabuya arajara*, as discussed by Reboucas-Spieker (1980), is closely related to *M. bistriata*, which has a disjunct distribution, being widespread in the Amazonian forest and occurring on the northern end of the Atlantic forest (states of Pernambuco and Alagoas). "There are no noticeable differences between eastern Hylaean and northeastern materials, but *arajara*, represented by over one hundred specimens, is undoubtedly different. The case is very probably one of speciation in a refuge, where morphological differentiation was faster than in the large forest areas" (Vanzolini 1981). In the case of some snakes, e.g., *Sibynomorphus mikanii*, differentiation also probably has occurred, but there were no adequate samples from the Atlantic forest to be compared with the series gathered in 1 week in the Cariris. Among the conclusions, the Cariris has been considered not only a refuge for the retreating forest elements, but also a refuge for species from open formations milder than *caatingas*, and in spite of the deforestation, the influence of surrounding *caatinga* fauna is marked but not excessively so.

SPECIATION ALONG THE ATLANTIC FOREST

Speciation patterns associated with hypothetical forest refuges during the dry and cold periods of the Pleistocene in the Atlantic forest domain have been discussed by Heyer (1984) and Jackson (1978), among others. Heyer and Maxson's (1983) analysis of frogs of the genus *Cycloramphus* seems most appropriate for the present discussion. The authors, based on morphological features (Heyer 1983) and information obtained using a microcomplement fixation technique of albumin, discussed the mechanisms of speciation within the genus. They considered the allopatric model of speciation to be the best to explain the patterns of the stream-associated species. They mentioned three kinds of events that could have acted as distributional barriers between contiguous populations of *Cycloramphus*, throughout the Cenozoic: (1) uplifting of the coastal mountains, resulting in changes of the local topography and stream drainage patterns; (2) worldwide climatic changes, particularly during the Pleistocene, causing alternate contraction and expansion of the Atlantic forest domain and its associated flora and fauna; (3) local extinctions due to landslides and other local catastrophes. Heyer and Maxson (1983) stressed that the "outstanding feature of the allopatric model of speciation for *Cycloramphus* was the small sizes of geographic areas of isolation and speciation. Each local area had a unique history in terms of geological formation (when and how they were formed), hydrology, extent of Atlantic forest cover during cooler and more arid times, and colonization, adaptations and extinctions of *Cycloramphus* populations."

The albumin data were found to be consistent with the hypothesis of Pleistocene speciation in forest refuges for two species lineages: (1) *Cycloramphus boraceiensis* and

dubius; and (2) *C. lutzorum*, *mirandariberioi*, and *rhyakonastes*. There is evidence from albumin data that all the other speciation events should be older than Pleistocene. The study of geographic variation of morphological characters within one species, *C. eleutherodactylus*, showed that although the information available was not complete, isolation and differentiation of the populations of *C. eleutherodactylus* in Pleistocene refuges would be a plausible explanation for the pattern of variation observed. Heyer and Maxson (1983) called attention to the need for geomorphological analysis in the area, to establish precisely where the refuges existed during the Quaternary. The refuges proposed for the southern part of the Atlantic forest by Ab'Saber (1977*b*) and Jackson (1978) do not coincide well with each other or with the *Cycloramphus* distribution pattern.

Most *Cycloramphus* species, with few exceptions, are forest-associated frogs. Among the exceptions, one species, *C. bandeirensis*, shows a mountaintop distribution well above the altitudinal limits of the Atlantic forest vegetation. Heyer and Maxson (1983) discussed the application of the "vanishing refuge model" of Vanzolini and Williams (1981) to explain the adaptation of this species to the open formation. As *C. bandeirensis* is closely related to other species occurring in the lower elevations of the Atlantic forest, it probably differentiated in situ. The vanishing refuge model is based on the frequent occurrence of edge-adapted forms of forest species. Such forms have a good chance of surviving the extinction of a refuge, becoming simultaneously adapted to open formations and geographically isolated from the populations surviving in refuges. It is a parsimonious mechanism to explain closely related but clearly independent species inhabiting adjacent contrasting environments.

DISCUSSION

Barton and Charlesworth (1984) claimed that "it is impossible to separate the effects of isolation, environmental differences and continuous changes by genetic drift from the impact of population bottleneck," in the examples given by Carson and Templeton (1984). They conclude that since all factors promote divergence, there is no need to invoke "additional influence of founder events." That the separation of all these factors is a difficult task does not necessarily imply that some of these factors do not exist. Bottleneck and founder events are not always coincident phenomena; a founder event is one special type of bottleneck, an instant bottleneck. In cases where a drastic reduction of population size happens in situ, the bottleneck may be either instantaneous (one generation) or gradual and take years (generations) to become effective.

Founder individuals (incidental, passive, or active migrators) and remainders of Carson's (1982) "disorganization in situ by reduction of population size to a vestige" may be either drawn by chance from a large population or selected due to certain determined special features. In this last case, founders blown by the wind should be light and stay in places where the wind could reach them. Active migrators are expected to have certain special genotypic endowments, while survivors of a drought or a lava flow, besides being carriers of given characteristics, would have to go through generations under these strong environmental pressures. Carson and Templeton (1984) mentioned that the genetic system most relevant to founder events is a cross-fertilizing diploid with a high recombination index. They supposed genetic systems that permit exuberant speciation in oceanic islands would have certain properties that would distinguish them from colonizing and cosmopolitan species. In some examples examined by these authors, a major segregating unit coupled with many epistatic modifiers was found to be part of the basic genetic architecture.

The most obvious difference between a founder event and a bottleneck event in situ is the spatial movement in the first case and the permanence in the same area in the second. An alternative situation could happen by a relatively widespread species being pushed or displaced into new areas during

periods of strong environmental pressures. The Amazonian groups, for instance, could have occupied the central areas and gradually been pushed to the periphery (where orographic forests would persist longer) while desiccation progressed. When speciation is being considered, dispersal and vicariance (fragmentation of species range), the two different types of historical explanation for present geographic patterns of organisms, from the spatial point of view, correspond to founder and in situ events.

How relevant is the impact of a new environment during the speciation process? Carson (1982), discussing the organizational changes in shifting balance systems, pointed out that "these changes do not always follow in lock-step the changes in the ambient environment, a fact that embarrasses the simplistic and poorly supported theory that every environmental change must be tracked by direct, fixed changes in the genetic structure of the species." The differences in floristic distribution and climate in the peripheral refuges of forest in northern South America would not be expected to be crucial for the differentiation of generalist species like *Drosophila paulistorum*, for instance.

I have pointed out some differences in time, genetic background and space between founder and other types of bottleneck events. There are, however, aspects common to these different types of situations as related to the mechanism of speciation. Evident differentiation from the ancestral population due to sampling effects may occur in all types of situations. Quoting from Mettler and Gregg's (1969) section on genetic drift: "Different paths will result from different path supplies... Since gene-frequency dispersion is cumulative and relatively permanent, drift may occur, not only in populations that remain small, but also in those that become small periodically [here, 'drift' equals the 'bottleneck effect'] or in those that are small at their inception, i.e., those established by a few emigrants, or founders carrying a small sample of genetic variation from a larger population [here, 'drift' equals the 'founder principle']."

Examining the above examples of speciation in South America, what could be considered under the scope of the "founder principle"? That speciation has occurred and is taking place in some groups is a fact. Evidence is strong in these examples for a relevant phase of isolation and drastic reduction of the population sizes sufficient to permit genetic reorganization.

The *Mabuya arajara* case seems to be an almost perfect example to demonstrate the relevance of bottleneck effects for speciation. Isolation, environmental differences, and continuous drift occurred in the three populations of the ancestral *M. bistriata* found in the Hylaea, the northern Atlantic forest, and the Cariris enclave. Significant divergence occurred only in the smaller population.

The most outstanding feature of *Cycloramphus* allopatric speciation was the small size of the geographical areas of isolation and differentiation from which one might infer that the effective population sizes were also small.

Obviously, the fragmentation of the forest and isolation of plants and animals in refuges only in certain cases resulted in differentiation, subspeciation, or speciation, while extinction and nondifferentiation was the result in other cases. Heyer and Maxson's (1982) analysis of the *Leptodactylus* complex of lowland frogs in Amazonia, for instance, revealed that speciation events seem to be Tertiary and not Pleistocene. The isolation in refuges accounts in this case for very few distributional events and for no speciation at all.

Among the cases discussed, genetic information is available only for the *Drosophila paulistorum* semispecies complex. Although nothing unusual or special has been discovered, the complex seems to have a genetic basic architecture favorable to undergoing speciation when a reduction of population to a "minimum size" is reached. The semispecies have been used in laboratory experiments of founding effects and linkage disequilibria (Powell and Richmond 1974).

Carson and Templeton (1984) have mentioned the use of *Drosophila mercatorum* in experimental investigations of the founder effect. They compared this neotropical

species to Hawaiian *Drosophila* and concluded that in both cases the same basic genetic architecture is found, "a type II architecture." *Drosophila mercatorum* is an intriguing example, since among the neotropical drosophilid fauna it could be considered as a "weed." It has been introduced to many areas and spread much beyond its original territory, indicating a colonizing bent that could be associated with a "general-purpose genotype."

In the South American cases reexamined here, there is no evidence of differentiation via founder or dispersal. Speciation events are associated to bottlenecks and not to isolation in large areas. Nevertheless, the pattern follow the orthodox mode of allopatric speciation which, at times, has been associated with the idea of large populations becoming divided into large sections. Haffer (1981, 1982) mentioned that the proportion of incipient species due to founder effects and range subdivision in South American continental faunas remains unknown. His studies of biogeographical aspects of the land bird fauna have led him to a "predominantly vicariant interpretation of differentiation patterns except for certain montane birds found on geologically independent mountain systems" (Haffer 1981).

Founder and bottleneck effects are descriptive expressions to indicate special types of situations observed in nature, obviously composed of many different aspects. In the South American examples, bottleneck can be identified as a factor distinct from isolation, environmental differences, or genetic drift.

Finally, I believe we must consider the matter of scale in space and time. The Hawaiian archipelago, from Niihau to the island of Hawaii, measures a total of approx. 650 km. The larger distances between neighboring islands range from about 50 to 150 km. The distances between Amazonian forest refuges during dry and cold periods were probably, in general, much larger than that, reaching 1000 km or more. In the Atlantic forest, on the contrary, distances could have been as short as between the Hawaiian Islands. When Carson and Templeton (1984), referring to continental areas, mention that "isolation would not be very great," all distances cannot be referred to the same standards.

A striking difference between many Hawaiian *Drosophila* and their continental relatives is the length of life cycles. South American *D. paulistorum* may have six to ten generations while a Hawaiian *Drosophila* would have one. The distribution pattern found in the *paulistorum* semispecies including large areas of sympatry may reflect the short life cycle. Hawaiian *Drosophila* would be more similar to South American lizards and frogs in that respect.

I have used vague terms such as "small," "moderately small," and "small enough," because these intuitive terms appear in other papers cited above. Barton and Charlesworth (1984) in their conclusions, for instance, would like to have distinguished between extremely "small populations" from "moderate populations size." How "small" is "small enough"? "Small enough" probably is different depending on the situation. The areas of peripheral Amazonian refuges were "small" for South American scale, but "extremely large" when compared to areas of the Hawaiian Islands.

Modeling in population genetics and genetics experiments in laboratories have added much to our understanding of population structures and their changes. Yet, much is to be done. Monitoring natural populations by using modern technology may be the next step.

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